

THE FAMILIES OF THE ORNITHISCHIAN DINOSAUR ORDER ANKYLOSAURIA

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ABSTRACT. All reasonably complete specimens of the ornithischian suborder Ankylosauria can be allocated to one of two families, the Ankylosauridae and the Nodosauridae, which differ in many anatomical features. Evolution within these two families was very conservative, with little morphological diversity. There is no truly 'primitive' ankylosaur that is morphologically suitable as a common ancestor for both families. *Scelidosaurus*, sometimes suggested as an ancestral ankylosaur, has no features diagnostic of the Ankylosauria. The origin of ankylosaurs is unknown, but the group may have an undocumented history extending back to the earliest beginnings of the Ornithischia.

MANY family groups have been proposed to subdivide the Ankylosauria, but few of these have been widely accepted. Study of excellent undescribed ankylosaur material at the American Museum of Natural History has revealed that there are two families within the Ankylosauria: the Ankylosauridae, typified by *Ankylosaurus*, *Euoplocephalus*, and *Pinacosaurus*; and the Nodosauridae, typified by *Nodosaurus*, *Panoplosaurus*, and *Sauropelta*. These two families show profound differences in almost every part of the skeleton. Virtually all known ankylosaurs can be classified in one or other of these two families, the only exceptions being fragmentary, incomplete specimens. Presented here is a brief survey of the diagnostic features of the suborder Ankylosauria with an account of important differences between the families Ankylosauridae and Nodosauridae.

The present paper is part of an extensive research programme on ankylosaurs that includes a revision of the sixty species of ankylosaurs, a general description of cranial and postcranial anatomy, endocranial anatomy, jaw muscles, teeth and diet, forelimb and hindlimb muscles, and function. A complete list of specimens examined during the course of this research is given in Appendix A.

Abbreviations. AMNH, American Museum of Natural History, New York; BM (NH), British Museum (Natural History), London; CM, Carnegie Museum, Pittsburgh; FMNH, Field Museum of Natural History, Chicago; GSM, Geologic Museum, Institute of Geologic Sciences, London; KU, University of Kansas Museum of Paleontology, Kansas; NMC, National Museum of Canada, Ottawa; NMNH, National Museum of Natural History, Washington; PU, Princeton University; ROM, Royal Ontario Museum; SMC, Sedgwick Museum, Cambridge; YPM, Yale Peabody Museum, New Haven.

TAXONOMIC USAGE

As used in this paper, the suborder Ankylosauria (= Thyreophora, in part, and Apraedentalia) contains two families: the Ankylosauridae (= Syrmosauridae) and the Nodosauridae (= Acanthopholididae, Polacanthidae, Hylaeosauridae, Palaeoscincidae, Struthiosaurinae, Panoplosaurinae, and Edmontoniinae; and all variants of these family group names, e.g. Acanthopholinae, Nodosaurinae). The family Ankylosauridae includes the following genera: *Ankylosaurus*, *Euoplocephalus*

(= *Dyoplosaurus*, *Scolosaurus*, and *Anodontosaurus*), *Pinacosaurus* (= *Syrmosaurus*), *Talarurus*, ?*Lametasaurus*, *Peishansaurus*, *Stegosaurides*, *Heishansaurus*, and *Saurophtes*. The family Nodosauridae includes the following genera: *Acanthopholis*, *Dysganus* (in part), *Hoplitosaurus*, *Hylaeosaurus* (= *Polacanthus* and *Polacanthoides*), *Nodosaurus* (= *Stegopelta* and *Hierosaurus*), *Palaeoscincus* (in part), *Panoplosaurus* (= *Edmontonia*) *Priconodon*, *Sauropelta*, *Silvisaurus*, and *Struthiosaurus* (? = *Crataeomus*, *Danubiosaurus*, *Leipsanosaurus*, *Pleuropeltis*, and *Rhodanosaurus*). The following genera are considered Ankylosauria, *incertae sedis*: *Loricosaurus*, *Brachypodosaurus*, and *Paranthodon*.

SYNOPSIS OF DIAGNOSTIC FEATURES

Skull: shape and external features

Ankylosauria in general: compared to other Ornithischia, ankylosaur skulls are relatively wide and dorsoventrally compressed (Pls. 11 and 12; text-figs. 1, 3, and 4). A posteriorly placed orbit is almost entirely surrounded by bony laminae that include a postorbital shelf separating the eye from the bulk of the mandibular musculature (Haas 1969). Some ossifications contributing to laminae enclosing the orbits are unique to ankylosaurs (Maryańska MS.). In all Ankylosauria the upper temporal fenestrae are closed by encroachment of surrounding skull elements (Maryańska 1971) and by co-ossified dermal plates (text-figs. 1, 3, and 4). Dorsal and lateral surfaces of the skull, as well as the lateral side of the mandible, are covered by co-ossified dermal plates which obscure cranial sutures in all but immature specimens (Maryańska 1971). *Panoplosaurus* has a large dermal plate over the cheek region (Pl. 12), a feature that might be common to all Ankylosauria. Ankylosaurs have a poorly developed prementary bone. There is a short retroarticular but no coronoid process on the mandible.

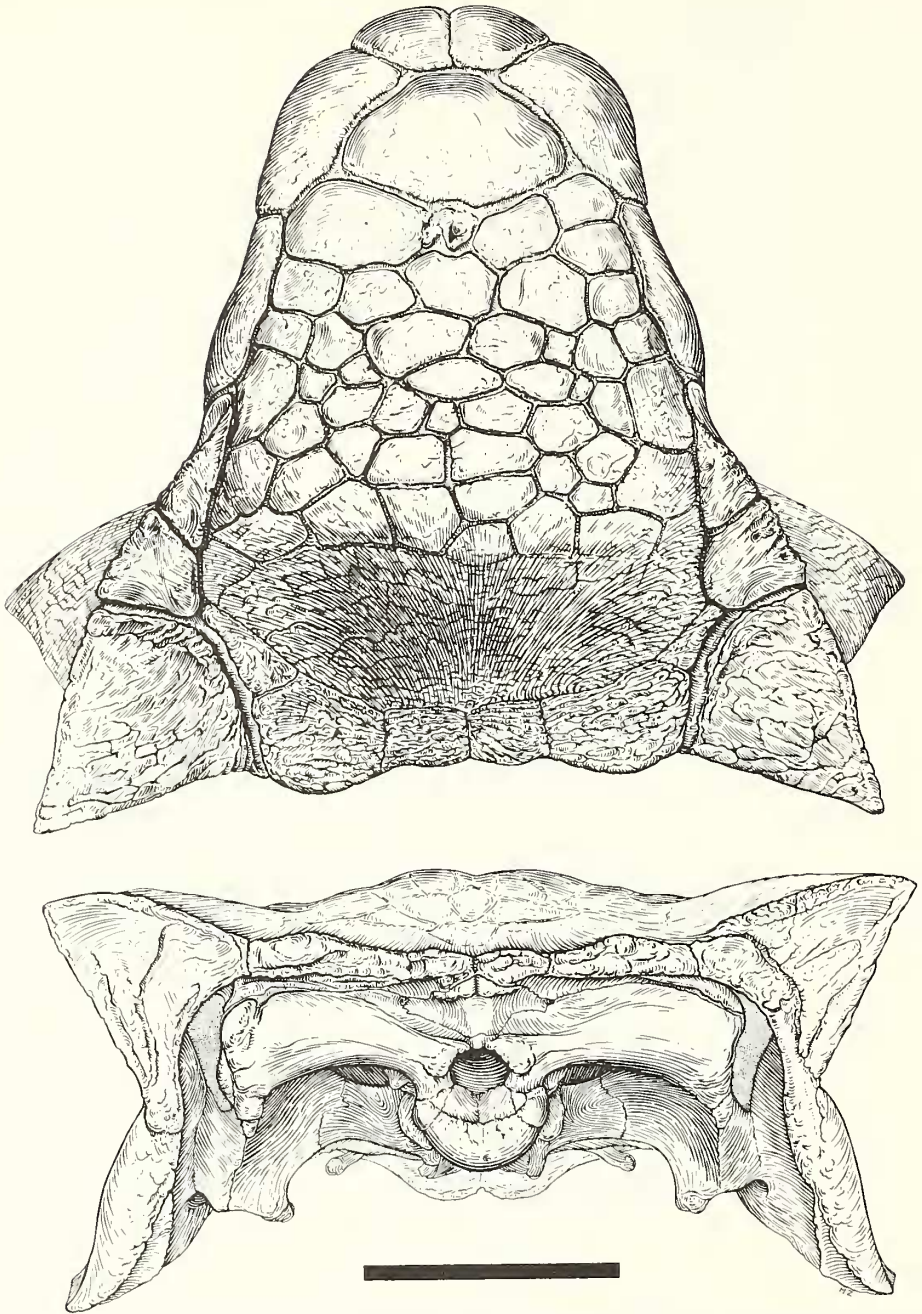
Ankylosauridae: ankylosaurid skulls are wide, roughly triangular in dorsal view with a broad, blunt anterior end (text-fig. 1). Maximum skull width always exceeds skull length. In most genera the posterior margin of the skull roof overhangs the occipital region so that the paroccipital processes are not visible in dorsal view. Bilateral symmetry is usually better maintained by larger dermal plates along the margins of the skull than by the numerous small ossicles over the snout (text-fig. 1). A pair of large dermal plates that are fused to the squamosals may be blunt or may form pointed, pyramidal, horn-like projections at the postero-lateral corners of the skull roof (Pl. 11; text-figs. 1, 3). A pair of ossicles above the nostrils are elongate and narrow in *Euoplocephalus* (text-fig. 3) and *Pinacosaurus*, but are large and plate-like in *Ankylosaurus* (Pl. 11; text-fig. 1). A large triangular dermal plate is fused to the jugal and quadratojugal postero-ventral to the orbit. Both the lateral temporal

EXPLANATION OF PLATE 11

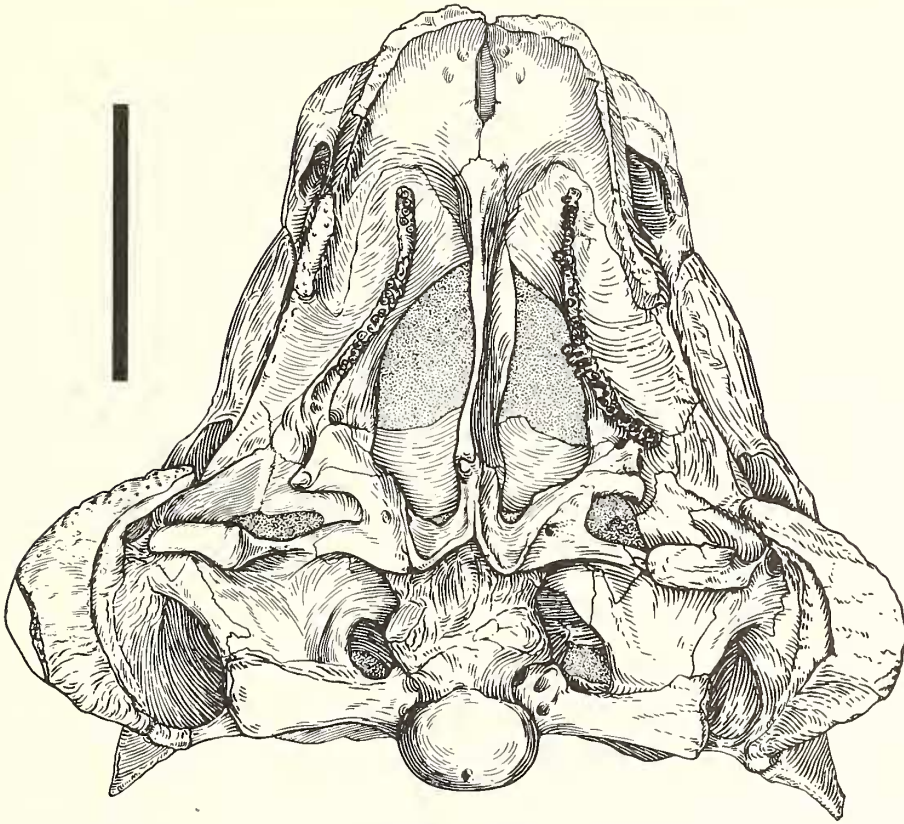
AMNH 5214, *Ankylosaurus magniventris*, skull and mandible; lateral view. Length of reference line = 10 cm.



COOMBS, ankylosaur dinosaurs



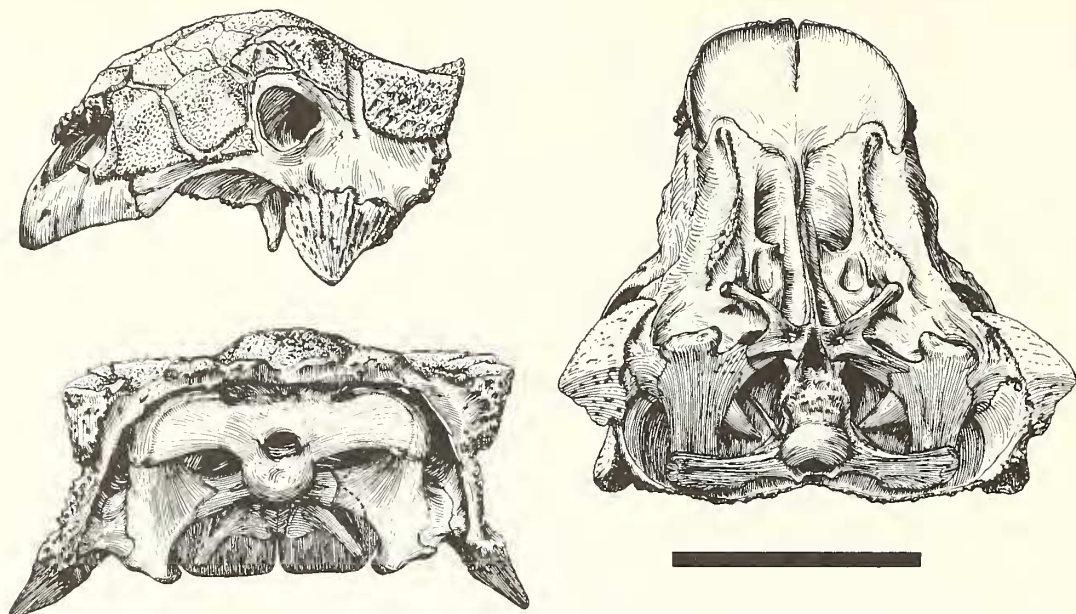
TEXT-FIG. 1. AMNH 5214, *Ankylosaurus magniventris*, skull; dorsal and posterior views.
Length of reference line = 20 cm.



TEXT-FIG. 2. AMNH 5214, *Ankylosaurus magniventris*, skull; ventral view. Length of reference line = 20 cm.

fenestra and the quadrate cotylus are hidden in lateral view by this large quadratojugal plate (Pl. 11; text-fig. 3).

Nodosauridae: nodosaurid skulls are elongate and pyriform in dorsal view with a narrower, more pointed anterior end than in ankylosaurids (text-fig. 4). Skull length always exceeds maximum skull width. Posteriorly directed distal ends of the paroccipital processes project beyond the skull roof and are visible in dorsal view (text-fig. 4). Dermal plates co-ossified to the skull roof are fewer in number and relatively larger than in ankylosaurids, and bilateral symmetry is generally maintained by all cranial plates. Grooves separating these dermal plates are obscure in larger nodosaurid skulls (presumably older individuals), whereas they are deeply incised in even the largest ankylosaurid skulls. Nodosaurids have a single, trapezoidal dermal plate anteriorly between the nostrils. No pyramidal plates and consequently no horn-like projections are present at the postero-lateral corners of the skull roof. Also, there is no large triangular plate on the quadratojugal and both lateral temporal fenestra and quadrate cotylus are therefore visible in lateral view (Pl. 11). *Silvisaurus* (KU 10296) was figured with the lateral temporal fenestra hidden by a wide jugal and



TEXT-FIG. 3. AMNH 5405, *Euoplocephalus tutus*, skull; lateral, posterior, and ventral views. Length of reference line = 20 cm.

quadratojugal, but the illustration is actually an antero-lateral view (Eaton 1960, fig. 1); the lateral temporal fenestra of *Silvisaurus* is exposed in lateral view as in other *Nodosauridae*.

Skull: palatal, basicranial, and occipital regions

Ankylosauria in general: ankylosaurs have a flat premaxillary shelf that forms a roof over the extreme anterior end of the palate (text-figs. 2-4). In many genera there is also a bony secondary palate posteriorly between the maxillary dental rows. Maxillary teeth are withdrawn medially creating a wide maxillary shelf laterally. The maxillary dental rows are curved as seen in ventral view (text-figs. 2-4).

Ankylosauridae: ankylosaurids have broad palates with a wide, short premaxillary plate anteriorly (text-figs. 2, 3). There is no ridge connecting the cutting edge of the premaxillary beak to the anterior end of the maxillary tooth row. All known *Ankylosauridae* have a complex secondary palate with two horizontal shelves composed of various palatal elements (text-figs. 2, 3, and 5). Thin, antero-laterally directed mandibular rami of the pterygoids arise close to the cranial midline. In most genera the

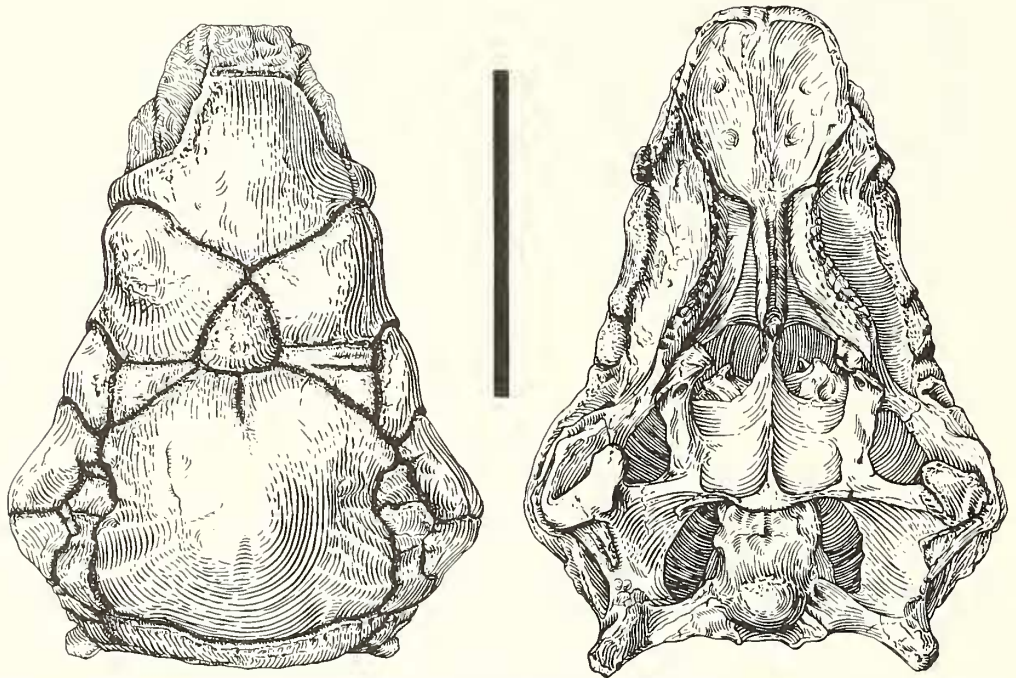
EXPLANATION OF PLATE 12

Upper: AMNH 5381, *Panoplosaurus*, skull and mandible; lateral view. *Lower*: NMC 2759, *Panoplosaurus mirus* (type specimen), skull and mandible; lateral view. Length of reference line = 10 cm.



COOMBS, ankylosaur dinosaurs

pterygoid-basisphenoid contact is not fused (exception: new Asiatic genus; Maryńska MS.). A backwardly opening foramen magnum and an oval, usually flat occipital condyle suggest that in life the head and neck had their long axes aligned as seen in lateral view. In most Ankylosauridae the quadrate, squamosal, and paroccipital



TEXT-FIG. 4. ROM 1215, *Panoplosaurus*, skull; dorsal and ventral views. Length of reference line = 20 cm.

process have articulation-like contacts (exception: bones are fused in a new Asiatic genus; Maryńska MS.).

Nodosauridae: nodosaurid palates are narrow and terminate anteriorly with a round to oval, commonly elongate premaxillary plate (text-fig. 4). A ridge connects the cutting edge of the premaxillae to the anterior end of the maxillary tooth row. Some genera have no secondary palate posterior to the premaxillae (e.g. *Sauropelta*, text-fig. 6C). Other genera have a single horizontal plate between the teeth (e.g. *Panoplosaurus*, text-figs. 4 and 6A, B). Nodosaurid pterygoids have a wide central plate with massive mandibular rami that arise laterally and project anteriorly approximately parallel to the midline (text-fig. 4B). In all known nodosaurid skulls the pterygoid and basisphenoid are fused together. A roughly spherical occipital condyle is set on a short, ventrally directed neck, and the foramen magnum opens somewhat ventrally suggesting that in life the skull was carried at a downward angle to the neck. Quadrate, squamosal, and paroccipital process are fused together in all Nodosauridae.

Skull: respiratory tract and cranial sinuses

Ankylosauria in general: the respiratory tract has no distinguishing features at the subordinal level.

Ankylosauridae: all ankylosaurids have complexly folded respiratory pathways within the cranium (text-fig. 5). Also, there is an extensive system of pouches and sinuses that are bounded both by normal cranial elements (vomeres, maxillae, premaxillae, etc.) and by new ossifications unknown in other fossil Reptilia (Maryńska MS.).

Nodosauridae: nodosaurids have simple paired respiratory passages within the cranium with no development of pouches or sinuses (text-fig. 6).

Teeth

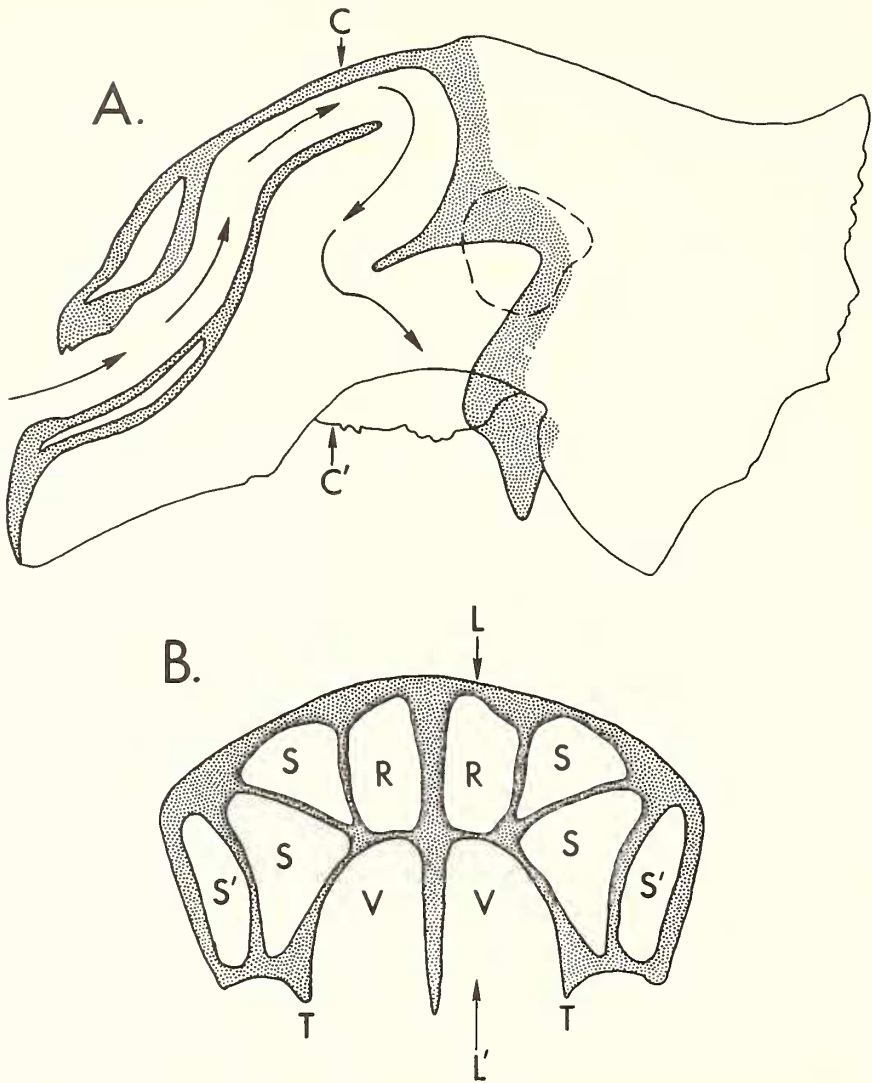
Ankylosauria in general: ankylosaur teeth are very small relative to skull size, with tiny crowns set on long, straight roots. Crowns are leaf-shaped, laterally compressed, and have equal numbers of cusps along anterior and posterior edges. Flanks of the crown are grooved or fluted and enamel is equally thick on labial and lingual surfaces. There are relatively few functional teeth in each maxilla and there are no more than two or three rows of replacement teeth. Adjacent teeth do not interlock to form a solid battery and do not align to form a single cutting edge. Ankylosaurs, along with stegosaurs and pachycephalosaurs, have the simplest and presumably most primitive teeth and tooth battery system among the Ornithischia.

Ankylosauridae: crowns of ankylosaurid teeth are very small both relative to their long roots and relative to skull size. Bases of the teeth are commonly swollen, but a distinct cingulum is rare. Fluting of the sides may be complex (e.g. *Euoplocephalus*). Premaxillary teeth are unknown in the Ankylosauridae.

Nodosauridae: nodosaurid teeth have larger crowns relative to root and skull size than ankylosaurid teeth. Bases of the crowns are only slightly inflated and well-defined basal cingula are common. Lateral fluting usually takes the form of parallel grooves that arise between cusps along the upper edge of the crown. *Sauropelta* (AMNH 3035), *Silvisaurus* (Eaton 1960), and possibly *Struthiosaurus* (Nopcsa 1928) have premaxillary teeth, but *Panoplosaurus* (Lambe 1919; Sternberg 1928; Gilmore 1930; Russell 1940) does not.

Vertebral column

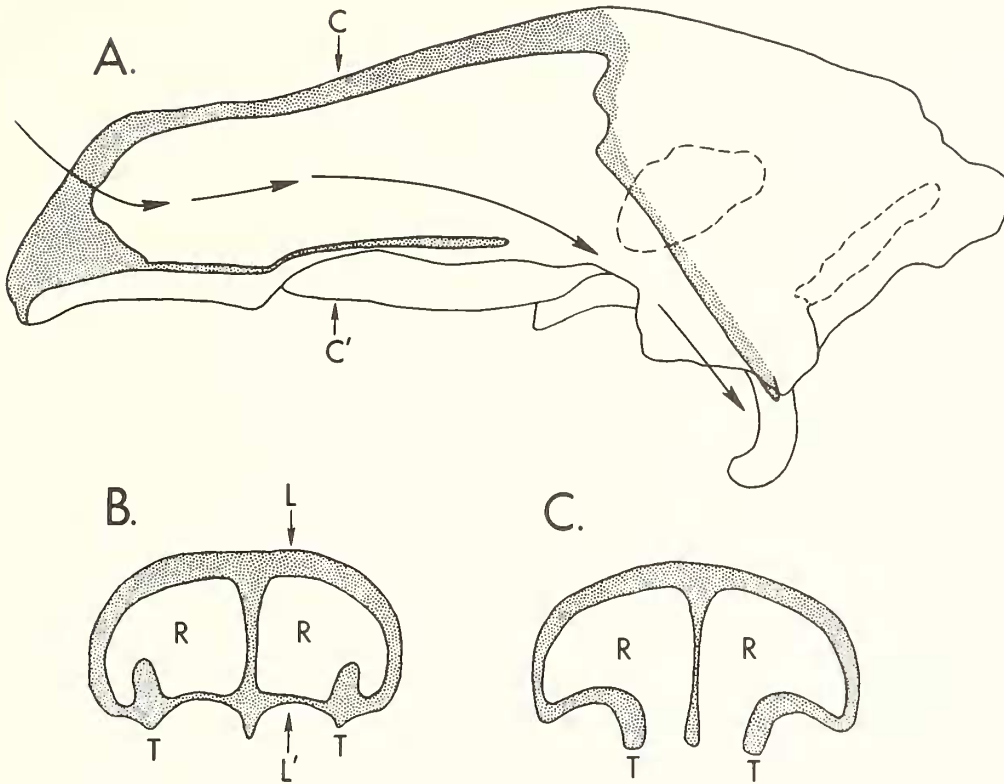
Ankylosauria in general: ankylosaur vertebral centra have expanded, amphiplatyan to amphicoelous articular faces. Neural arches are low and neural spines are moderately tall. Centra of presacral vertebrae have lengths subequal to their maximum diameters; most caudal centra are shorter than their diameters. Transverse processes of dorsal vertebrae are inclined upwards and outwards, but not to the degree seen in *Stegosaurus*, and dorsal ribs, T-shaped in section, are commonly fused to both transverse process and centrum. The last four or five dorsals co-ossify and fuse to the sacrum to form a presacral rod. Ribs fused to the presacral rod contact and help support the hypertrophied pre-acetabular process of the ilium. One or two proximal caudals are sometimes fused to the sacrum and commonly have massive transverse processes that contact the abbreviated postacetabular process of the ilium (text-fig. 12).



TEXT-FIG. 5. Diagrammatic sections through *Euoplocephalus* skulls showing respiratory passages and cranial sinuses. Based on several specimens.

A, parasagittal section with main respiratory path indicated by arrows and position of orbit indicated by broken line. B, cross-section. Abbreviations: C-C', level of cross-section shown in B; L-L', level of parasagittal section shown in A; R, main respiratory tract; S, cranial sinus; S', maxillary sinus; T, tooth row; V, palatal vault.

Ankylosauridae: articular faces of most ankylosaurid centra are flat, but a few posterior dorsals may have a centrally positioned knob on the articular face. Atlas and axis are separate in *Pinacosaurus* and *Euoplocephalus* but are fused in other genera (new Asiatic genus; Maryńska MS.). Distal caudal vertebrae are large and highly modified in connection with presence of a tail club. Long prezygapophyses

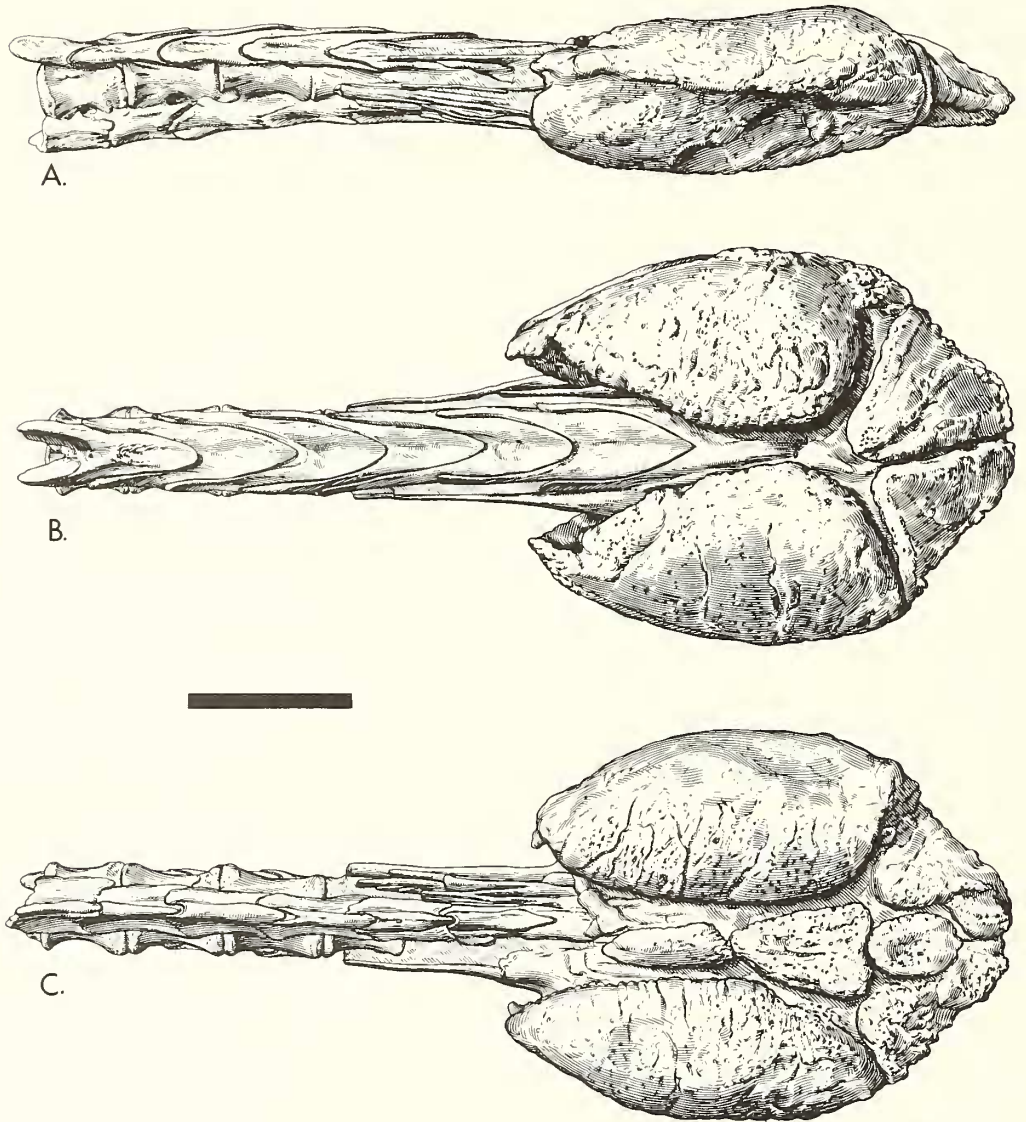


TEXT-FIG. 6. Diagrammatic section through nodosaurid skulls showing respiratory passages. A, parasagittal section based on several *Panoplosaurus* skulls. The respiratory path is shown by arrows. Positions of the eye and lateral temporal fenestra indicated by broken lines. The nostril lies lateral to the plane of this section and thus the respiratory tract appears to be closed anteriorly. B, cross-section through the snout of *Panoplosaurus*, based primarily on AMNH 3076. Ridges protruding into the respiratory passages contain enamel organs, replacement teeth, and roots of functional teeth. C, cross-section through the snout of *Sauropelta*, restored from the badly crushed skull of AMNH 3035. *Sauropelta* lacks a secondary palate posterior to the premaxillary shelf. Abbreviations: C-C', level of cross-sections shown in B and C; L-L', level of parasagittal section shown in A; R, respiratory tract; T, tooth row.

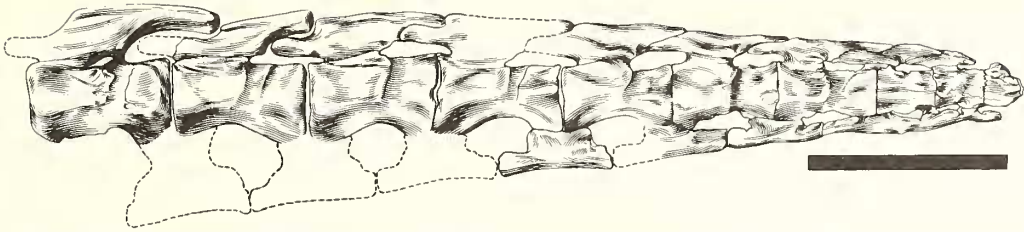
and long flattened postzygapophyses of posterior caudals extensively overlap one another and effectively immobilize the distal third of the tail (text-fig. 7). Neural arches of distal caudals, measured from the extreme tips of pre- and postzygapophyses, may be twice the length of their centra. Haemal arches of distal caudals are low, elongate, tube-like, and have zygapophyseal-like interlocking articulations (text-fig. 7A, C). In some specimens the centra of posterior dorsals fuse into a solid rod (Maryńska 1969).

Nodosauridae: posterior dorsal and proximal caudal vertebrae of nodosaurids usually have a median, knob-like projection on the articular faces of the centra (notochordal projection of Gilmore 1930). Atlas and axis vertebrae may be fused

(*Panoplosaurus*) or free (*Sauropelta*, *Struthiosaurus*). Caudal vertebrae are progressively smaller towards the distal, clubless end of the tail (text-fig. 8). Zygapophyses of distal caudals are relatively much shorter than in Ankylosauridae. There is contact between successive haemal arches through about the distal half of a nodosaurid tail, but there are no interdigitating articulations, and the arches extend further from their centra than in Ankylosauridae (text-fig. 8).



TEXT-FIG. 7. AMNH 5214, *Ankylosaurus magniventris*, distal caudal vertebrae with terminal tail club. A, lateral view. B, dorsal view. C, ventral view. Length of reference line = 20 cm.

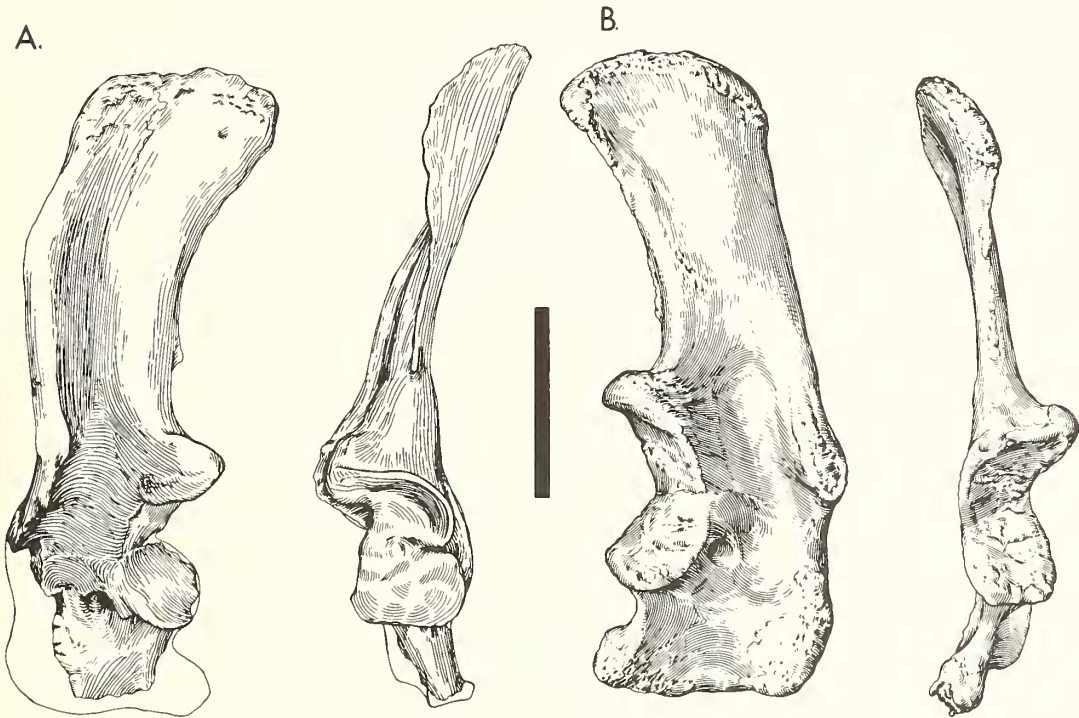


TEXT-FIG. 8. AMNH 3032, *Sauropelta edwardsi* (type specimen), distal end of tail. Length of reference line = 10 cm.

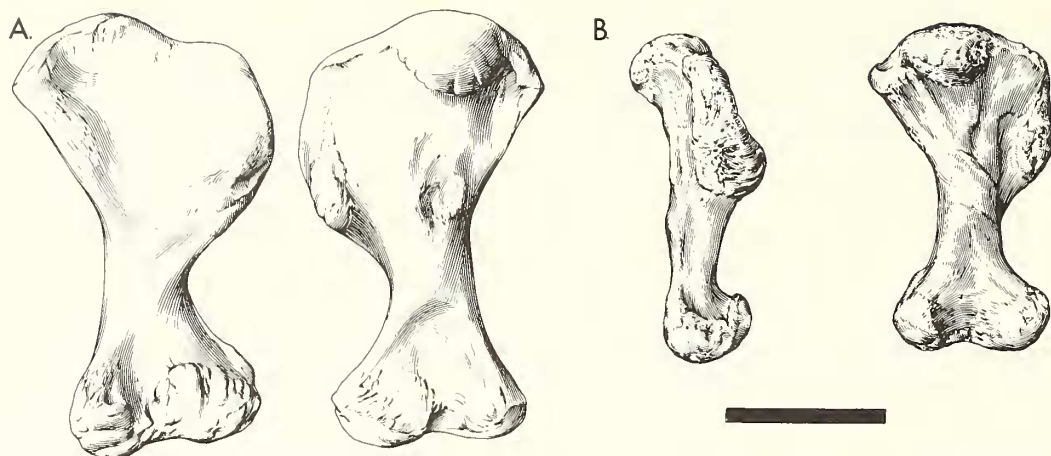
Pectoral girdle and forelimb

Ankylosauria in general: in most ankylosaurs the scapula and coracoid are co-ossified (exceptions: *Struthiosaurus*, *Hylaeosaurus*). The massive forelimbs are two-thirds to three-quarters the length of the hindlimbs. A long olecranon process accounts for one-quarter to one-third the entire length of the ulna.

Ankylosauridae: ankylosaurid scapulae are relatively long, the coracoids relatively small compared with nodosaurid elements. There is a ridge-like spine along the extreme anterior edge of the scapula (text-fig. 9). A pair of roughly triangular sternal



TEXT-FIG. 9. A, AMNH 5895, *Ankylosaurus magniventris* (type specimen), scapulocoracoid; lateral and posterior views. B, AMNH 5424, *Euoplocephalus*, scapulocoracoid; lateral and posterior views. Length of reference line = 20 cm.



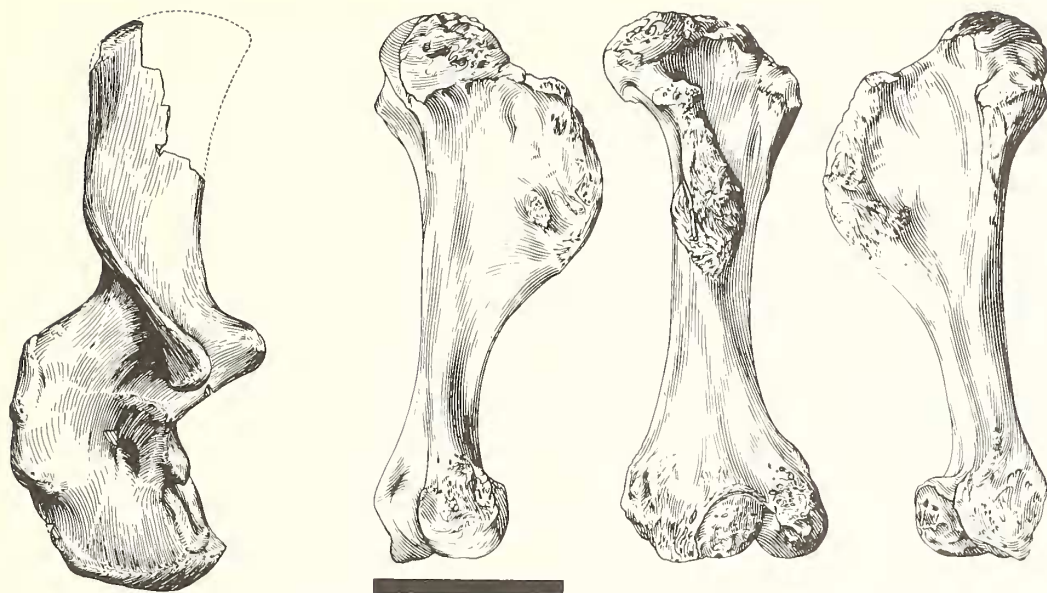
TEXT-FIG. 10. A, AMNH 5214, *Ankylosaurus magniventris*, left humerus; ventral and dorsal views. B, AMNH 5404, *Euoplocephalus*, right humerus; lateral and dorsal views. Length of reference line = 20 cm.

plates is fused along the ventral midline to form a single, rhomboidal plate (Maleev 1954, fig. 6). Massive ankylosaurid humeri have a very large pectineal crest that usually terminates at or slightly distal to humeral mid-length (text-fig. 10). A rather flat radial capitulum on the humerus has an oval outline that corresponds to the oval cross-section of the radius.

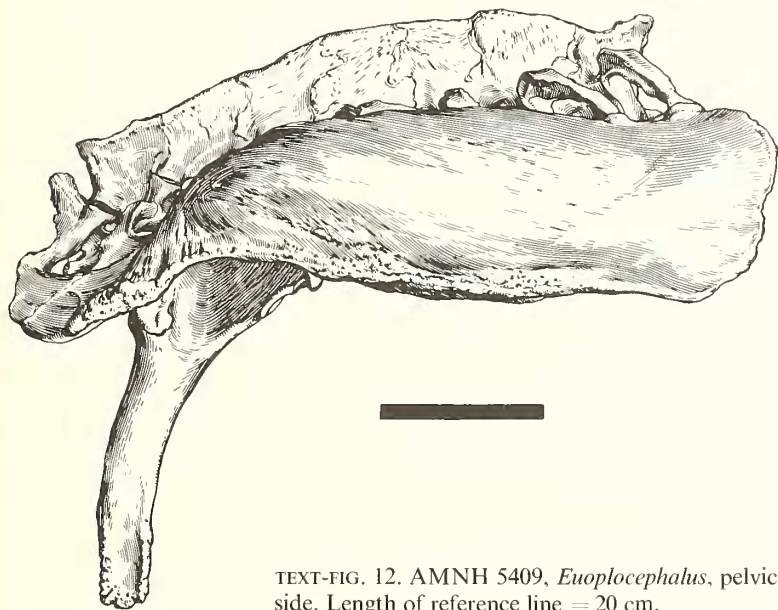
Nodosauridae: nodosaurid scapulae are relatively short and slender and the coracoids relatively very large compared with ankylosaurid elements (text-fig. 11). A knob-like scapular spine overhangs the coracoid and is positioned either centrally on the scapular blade or far posteriorly near the glenoid notch (text-fig. 11). Anterior to the scapular spine is a supraspinous fossa formed by coracoid and scapula. In the primitive nodosaurid *Hylaeosaurus* the scapular spine is positioned posteriorly, near the glenoid, but is ridge-shaped rather than knob-like and there is no supraspinous fossa. Nodosaurid sternal plates are narrower than ankylosaurid plates and are not fused along the midline (Eaton 1960, incorrectly identified as a pubis, see Ostrom 1970, p. 114). Nodosaurid humeri appear longer and more slender than those of ankylosaurids primarily because the pectineal crest commonly terminates more proximally (text-fig. 11). The radial capitulum is a subspherical knob that rises well above the humeral shaft, and the radius is almost circular in cross-section.

Pelvic girdle and hindlimb

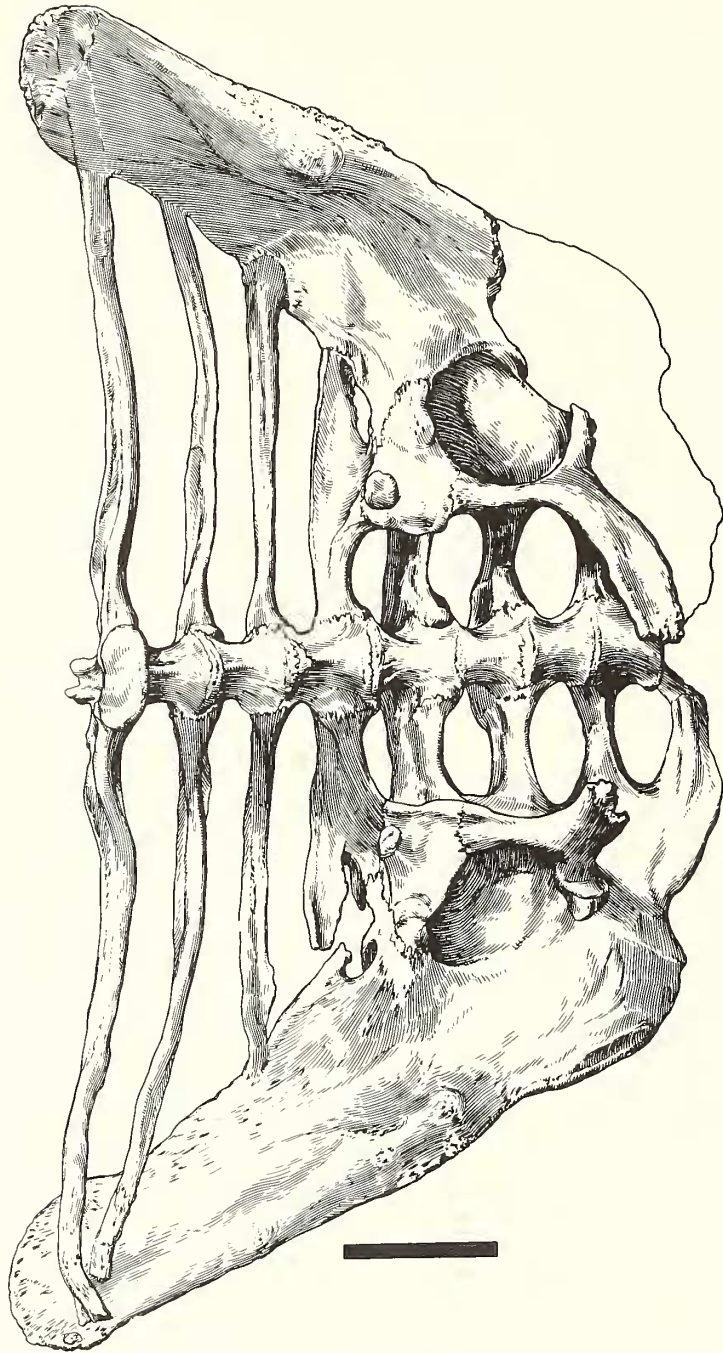
Ankylosauria in general: ankylosaur ilia are twisted so that the primitive lateral surface faces ventrally or ventromedially and the ilium overhangs the femur (text-figs. 12–14). The pre-acetabular segment of the ilium is very long and diverges from the vertebral column anteriorly (text-fig. 12); the postacetabular segment is short. The tiny, block-like pubis has a short, finger-like postpubic process but no distinct prepubic process. The acetabulum, which is always imperforate, is formed almost entirely by ilium and ischium (illustrations of ankylosaur pelves given by Brown 1908 and von Huene 1956, are incorrect). The massive femur is 30% longer than the equally massive tibia.



TEXT-FIG. 11. *Left*: YPM 5179, *Sauropelta edwardsi*, scapulocoracoid; lateral view. *Right*: AMNH 3032, *Sauropelta edwardsi* (type specimen), right humerus; lateral, ventral, and medial views. Length of reference line = 20 cm.



TEXT-FIG. 12. AMNH 5409, *Euoplocephalus*, pelvic girdle; lateral view of right side. Length of reference line = 20 cm.



TEXT-FIG. 13. AMNH 5409, *Euoplocephalus*, pelvic girdle; ventral view.
Length of reference line = 20 cm.

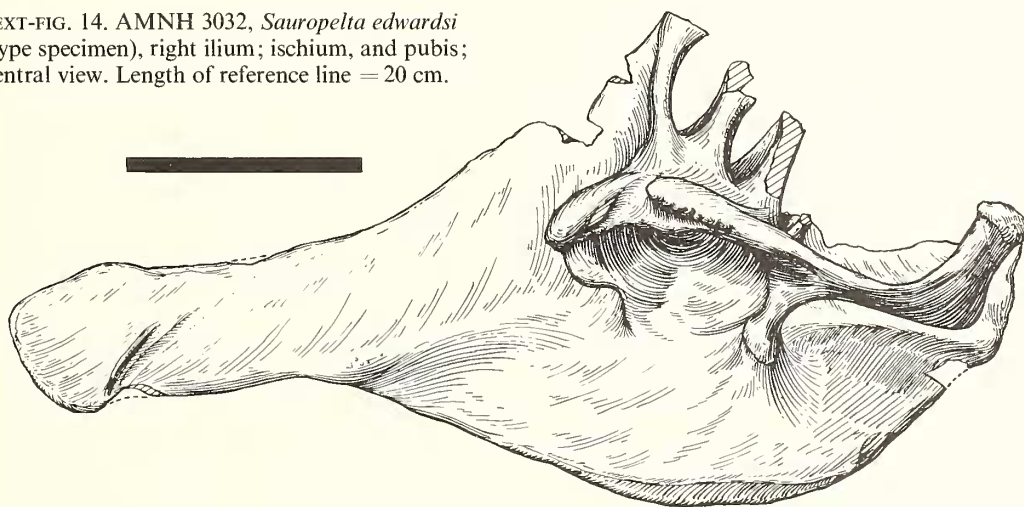
Ankylosauridae: the pre-acetabular segment of the ilium of ankylosaurids is broad and twisted such that the primitive lateral surface faces ventromedially. The post-acetabular segment of the ilium is very short (text-fig. 12). A straight or slightly curved ischium descends almost vertically from the acetabulum (text-fig. 13). There is little distinction between the terminally positioned femoral head and the proximal femoral trochanters (text-fig. 15). Insertion of the coccygeofemoralis muscles (fourth trochanter) is distal to the femoral mid-length (text-fig. 15).

Nodosauridae: in nodosaurids the pre-acetabular segment of the ilium is somewhat shorter and narrower and the postacetabular segment somewhat longer than in ankylosaurids (text-fig. 14). The pre-acetabular part is twisted into a horizontal plane and consequently the primitive lateral surface faces ventrally. Nodosaurid ischia extend postero-ventrally from the acetabulum and have a sharp flexion near the middle that turns the distal end straight downwards (text-fig. 14). There is a slight displacement of the femoral head medially, and proximal femoral trochanters are more distinct than in ankylosaurids (text-fig. 16). The fourth trochanter is always on the proximal half of the femur.

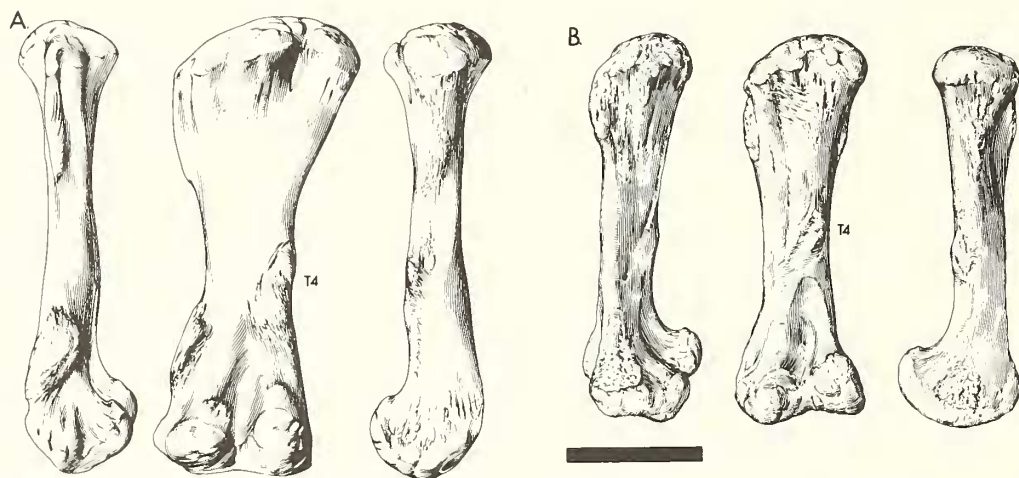
Postcranial armour

Ankylosauria in general: ankylosaurs have an extensive postcranial armour composed of oval keeled plates set into a continuous, mosaic of interlocking small, flat ossicles. Keeled plates are commonly arranged in transverse rows and keels of larger plates may be higher and sharper towards the flanks of the body. Anteriorly, the first two transverse rows of plates are fused to underlying half-rings of bone to form two cervical half-rings. Median dorsal plates of the third transverse row are fused together in some genera (e.g. *Panoplosaurus*). Brown (1908) restored *Ankylosaurus* with longitudinally arranged keeled plates, and Nopcsa (1929) restored *Struthiosaurus* with seven anterior cervical collars and numerous caudal rings, but both of these restorations are entirely hypothetical and unsubstantiated.

TEXT-FIG. 14. AMNH 3032, *Sauropelta edwardsi* (type specimen), right ilium; ischium, and pubis; ventral view. Length of reference line = 20 cm.

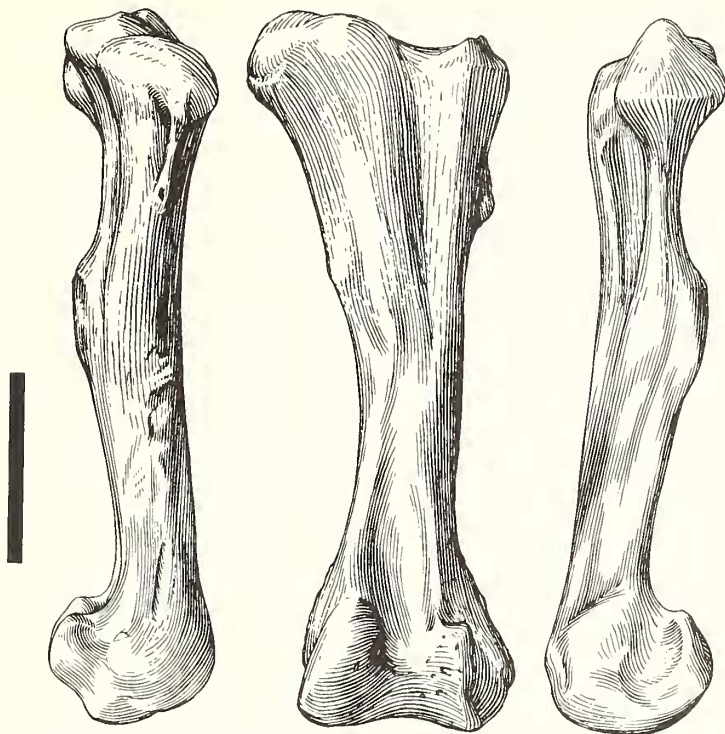


Ankylosauridae: oval keeled plates of ankylosaurids are deeply excavated on the inner surface so that the plates are relatively thin and light. Median keels of these plates may be tall, but plate height never exceeds maximum basal diameter. Some plates are shaped like low, obtusely pointed cones that have been laterally compressed. Cross-sections of such plates are lenticular or lozenge-shaped. Keeled dermal plates fused to cervical half-rings do not contact each other and retain the typical oval outline of keeled plates from other areas of the body. Two massive plates which may be blunt or pointed, and a variable number of smaller ossicles form a large, terminal tail club (text-fig. 7).



TEXT-FIG. 15. A, AMNH 5214, *Ankylosaurus magniventris*, left femur; lateral, posterior, and medial views. B, AMNH 5404, *Euoplocephalus*, left femur; lateral, posterior, and medial views. Position of fourth trochanter is indicated at T4. Length of reference line = 20 cm.

Nodosauridae: inner surfaces of nodosaurid keeled plates are flat or only slightly excavated and the plates are therefore thicker and heavier than similar ankylosaurid plates. In addition to oval keeled plates and compressed conical plates, nodosaurids have tall conical spikes or spines that have heights at least twice the maximum basal diameter and that are oval to circular in cross-section. Some of these spines formed a low horizontal row along the side of the body (Matthew 1922). Some Nodosauridae also have taller spikes with heights of up to five times their basal diameter and which are very similar to *Stegosaurus* caudal spines. Where these spikes were positioned on nodosaurids is uncertain, but limited evidence suggests they were on the flanks of the body and not on the tail. Keeled plates of nodosaurid cervical half-rings contact each other and are rectangular or square in outline. Nodosaurids do not have a tail club.



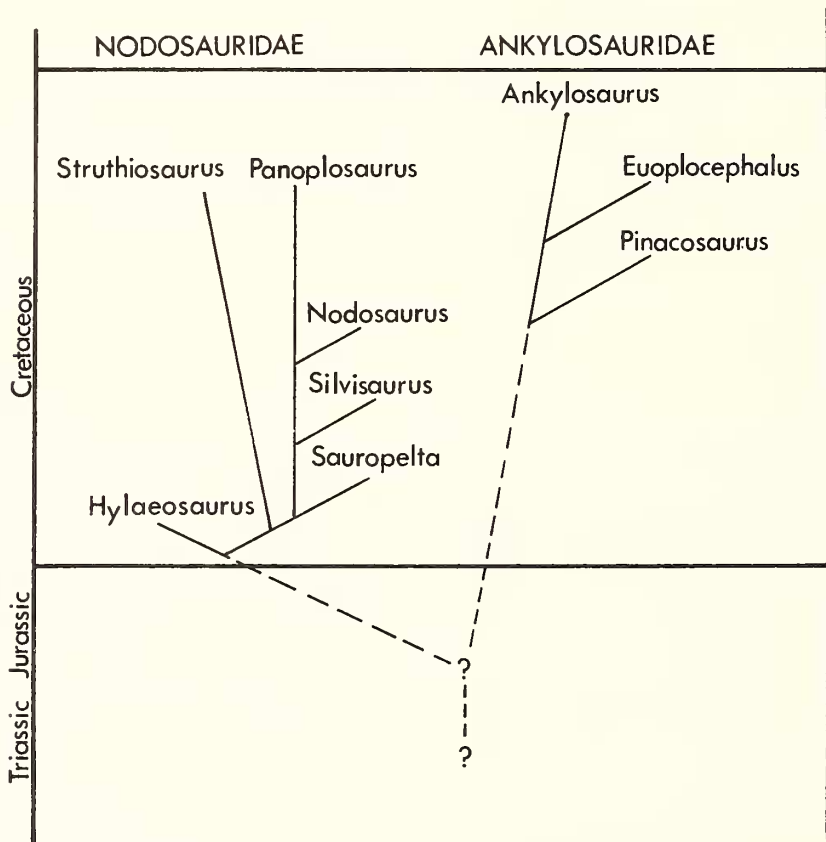
TEXT-FIG. 16. AMNH 3032, *Sauropelta edwardsi* (type specimen), left femur shown reversed; lateral, posterior, and medial views. Length of reference line = 20 cm.

DISTRIBUTION AND EVOLUTION

Ankylosaurians are present in most Cretaceous formations that yield dinosaurs (see Appendix B for complete list with references), but are unknown in Jurassic formations. The distribution of the two families is different. Nodosauridae are present in Europe from Neocomian (Wealden Beds) to Campanian (Middle Gosau Beds and Ajka Beds) and are present in North America from Neocomian or Aptian (Arundel Formation to Campanian or earliest Maestrichtian (Mbr. A of Edmonton Formation and Bearpaw Shale). There is a single tooth (AMNH 5008) from the late Maestrichtian (Hell Creek Formation) that may belong to a nodosaurid. Nodosauridae are not present in Asia. Ankylosauridae are present in Asia from Coniacian or Santonian (Djadochta Formation) to late Campanian or early Maestrichtian (Upper Nemegt Formation) and are present in North America from Campanian (Two Medicine Formation, Judith River Formation, Oldman Formation) to late Maestrichtian (Hell Creek Formation, Mbr. E of Edmonton Formation). Ankylosauridae are not present in Europe. Ankylosaur specimens from South America ('Estratos con Dinosaurios') are too fragmentary for positive assignment to one of the two families.

Evolution of the Nodosauridae is very conservative, with little morphologic diversity. The six genera that are known from reasonably complete material can be arranged into three groups or lineages (text-fig. 17). *Hylaeosaurus* is unique and primitive among Nodosauridae in lacking a supraspinous fossa. The scapular spine is displaced posteriorly as in all Nodosauridae, but muscular changes leading to formation of the supraspinous fossa have not developed. *Hylaeosaurus* is also primitive in having the scapula and coracoid separate rather than fused together, a feature shared with *Struthiosaurus*. The small size of the type specimen of *Hylaeosaurus* is responsible for the erroneous idea that the genus is small (e.g. Romer 1956, 1968; Steel 1969). Isolated elements referable to *Hylaeosaurus* (e.g. BM (NH) R1106, R1107, 2602a, and 2615) indicate a maximum size approaching that of the largest Nodosauridae.

Struthiosaurus appears to be the terminus of a European lineage that is represented in the early Cretaceous by specimens described under the name '*Acanthopholis*' (here regarded as a *nomen dubium*). These nodosaurids are characterized by small size, premaxillary teeth (?), and a separate coracoid and scapula. Unlike *Hylaeosaurus*



TEXT-FIG. 17. Relationships of the major genera of the Ankylosauria.

there is a fully developed supraspinous fossa. Whether the small size (about one-quarter in linear dimensions the size of typical North American Nodosauridae) of this *Struthiosaurus* group is primitive (Romer 1956, 1968; Steel 1969) or secondary is unclear. There does not appear to be an over-all trend towards large size in the Nodosauridae in so far as the earliest North American genus (*Sauropelta*, Aptian or Albian, Cloverly Formation) is one of the largest nodosaurids. The concept that *Struthiosaurus* and '*Acanthopholis*' are more lightly armoured (Romer 1956, 1968; Steel 1969) than North American nodosaurids is incorrect. The extent to which armour covers the body is about the same in all Nodosauridae.

North American Nodosauridae form a third group characterized by uniformly large size, co-ossified coracoid and scapula, and fully developed supraspinous fossa. Early forms (*Sauropelta* and *Silvisaurus*; text-fig. 17) retain premaxillary teeth, but these are lost in late Cretaceous *Panoplosaurus*. *Panoplosaurus* is also advanced in that the atlas and axis vertebrae are fused, whereas these vertebrae are separate in most ankylosaurs (*Sauropelta*, *Struthiosaurus*, and the ankylosaurids *Pinacosaurus* and *Euoplocephalus*).

Unique derived characters that distinguish nodosaurids from all other Ornithischia, including Ankylosauridae, include fusion of the squamosal, paroccipital process, and dorsal end of the quadrate; a scapular spine displaced posteriorly to near the glenoid notch; and a sharp flexion near mid-length of the ischium. Because of these features, no member of the Nodosauridae is morphologically suitable as an ancestor for the Ankylosauridae.

Three genera of the Ankylosauridae are known from reasonably complete specimens, and these indicate an even more conservative evolution than in the Nodosauridae. When arranged according to relative geologic age (text-fig. 17), there is a regular size increase from *Pinacosaurus* through *Euoplocephalus* to *Ankylosaurus* (maximum skull lengths, respectively = 305, 460, and 760 mm). *Ankylosaurus* was the last and largest of all the Ankylosauria. *Pinacosaurus* retains in its pes the primitive ornithischian phalangeal formula of 2-3-4-5-(?)0, while *Euoplocephalus* is advanced in having lost pes digit 1 including the metatarsal. In *Pinacosaurus* and *Euoplocephalus* the nostril is an elongate slit divided by a vertical septum that separates the main respiratory path from a more lateral maxillary sinus, and the premaxillae of these genera are not covered by dermal plates (see lateral view in text-fig. 3). In *Ankylosaurus* the nasal bone and/or a dermal plate fused to the dorsal margin of the nostril has expanded anteriorly and laterally over the narial opening and premaxillae. Thus in *Ankylosaurus* the premaxillae are covered by dermal plates and the nostril is a small circular opening that lies far laterally on the snout (Pl. 12).

Unique derived characters that distinguish ankylosaurids from all other Ornithischia, including Nodosauridae are: horn-like projections formed by dermal plates at the postero-lateral corners of the skull roof; lateral temporal fenestrae hidden below expanded quadratojugal and co-ossified dermal plates; a complex system of cranial sinuses; and a terminal tail club supported by highly modified distal caudal vertebrae. Because of these features, no member of the Ankylosauridae is morphologically suitable as an ancestor for the Nodosauridae.

Because all genera of the Ankylosauridae and all genera of the Nodosauridae have derived characters diagnostic of their respective families, it might reasonably be

questioned whether the two families of the Ankylosauria have a common ancestry. However, the families Ankylosauridae and Nodosauridae share the following unique derived characters that set them apart from other Ornithischia and justify their unification in a suborder Ankylosauria: skull covered by co-ossified dermal plates; upper temporal fenestrae closed by encroachment of surrounding skull bones and co-ossified dermal plates; postorbital shelf formed; presacral rod formed; ilia twisted into horizontal plane; pre-acetabular ilium long and broad; block-like pubis with short, finger-like postpubic process and no distinct prepubic process; and extensive armour of keeled plates includes two cervical half-rings with co-ossified keeled plates. The only one of the preceding features that is found in other ornithischians is closure of the upper temporal fenestrae, which has taken place independently in pachycephalosaurs (Brown and Schlaikjer 1943; Galton 1971; Maryńska and Osmolska 1974). Therefore the Ankylosauridae and Nodosauridae must have some unknown common ancestor, probably in the pre-Cretaceous Mesozoic (text-fig. 17). Phylogenetic divergence of the two families, and evolution of the numerous morphologic differences between them are not documented by currently known fossils.

If the common ancestor of the two ankylosaur families is unknown, the origin of the Ankylosauria as a whole is even more obscure. *Scelidosaurus* has been proposed as an ancestral ankylosaur on the basis of its exceedingly short prepubic process (Romer 1968; Thulborn 1971a), an opinion based upon a referred specimen (Rixon 1968; Charig 1972) that may not belong to *Scelidosaurus*. The pelvis of this alleged *Scelidosaurus* has a long postpubic process, a perforate acetabulum, a short, pointed pre-acetabular ilium, and a broad, vertical postacetabular ilium (Charig 1972, fig. 2), all features unlike ankylosaur pelvic structure. Overall, the pelvis of this alleged *Scelidosaurus* is more reminiscent of hypsilophodontid Ornithopoda (Thulborn 1974), except that the short prepubic process is similar to that of *Protoceratops* (Brown and Schlaikjer 1940). Ankylosaur pubes (Gilmore 1930; Ostrom 1970) bear no special similarity to that of the alleged *Scelidosaurus*. The type of *Scelidosaurus* (*vide* Newman 1968) has ankylosaur-like armour plates, but lacks the diagnostic cervical half-rings. The upper temporal fenestrae of *Scelidosaurus* are open, and there are no armour plates fused to the skull roof (Owen 1863). *Scelidosaurus* has a single supernumerary cranial element above the orbit (Coombs 1972), whereas *Pinacosaurus* and presumably other Ankylosauridae have three (Maryńska 1971). Nodosaurid skull roof composition is unknown. Therefore, *Scelidosaurus* is not morphologically suitable as an ancestor for the family Ankylosauridae, and in so far as no features diagnostic of the Ankylosauria have yet been described in *Scelidosaurus*, I do not accept the genus as an ancestor for any ankylosaurs. (See note added in proof, p. 168.)

Stegosaurs have often been proposed as close relatives of ankylosaurs because both groups are quadrupedal and armoured (Marsh 1889, 1892; Huene 1909; Nopcsa 1915, 1917, 1918, 1923; Hennig 1915, 1924; Lapparent and Lavocat 1955). *Stegosaurus* has three 'palpebrals' (Coombs 1972) or 'supraorbitals' (Gilmore 1914) arranged similarly to those of the ankylosaurid *Pinacosaurus* (Maryńska 1971) but whether this is a derived character shared by stegosaurs and ankylosaurs, an independent development in each suborder, or the retention of a primitive structure is unclear (Coombs 1972). Stegosaur pelvic morphology is strikingly unlike that of ankylosaurs (Romer 1927). Ankylosaurs share with stegosaurs and pachycephalosaurs

the simplest and, by inference, most primitive tooth morphology and arrangement within the Ornithischia. Even relatively 'primitive' Ornithopoda such as *Fabrosaurus* (Thulborn 1971*b*), *Heterodontosaurus* (Crompton and Charig 1962), and *Hypsilophodon* (Swinton 1936; Galton 1974) have asymmetrically distributed enamel, precise alignment of teeth, and initial development of close-packing of replacement teeth, the latter eventually developing into the complex tooth-batteries of hadrosaurs. Also, ankylosaurs are the only Ornithischia with an imperforate acetabulum, possibly a retained primitive feature extending back to pseudosuchians.

Therefore, both the ancestry of ankylosaurs and their connection to other Ornithischia, including stegosaurs, is exceedingly remote from all currently known ankylosaur fossils both temporally and morphologically. At present, the origin of ankylosaurs remains an open question.

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Note added in proof. Since this paper went to press an article has been published suggesting the reclassification of *Scelidosaurus* within the Ornithopoda. (Thulborn, R. A. 1977. Relationships of the Lower Jurassic dinosaur *Scelidosaurus harrisonii*. *J. Paleont.* **51**, 725-739, 6 figs.)

APPENDIX A

During the course of this study, I personally examined type specimens of the following ankylosaur taxa:

Acanthopholis horridus Huxley, 1867 (GSM 109046–GSM 109058); *A. eucercus* Seeley, 1869 (SMC 55552–SMC 55557); *A. macrocercus* Seeley, 1869 (SMC B55588–B55609); *A. platypus* Seeley, 1869 (SMC B55449–B55461); *A. stereocercus* Seeley, 1869 (SMC B55558–B55569); *Ankylosaurus magniventris* Brown, 1908 (AMNH 5895); *Anodontosaurus lambei* Sternberg, 1929 (NMC 8530); *Dyoplosaurus acutosquameus* Parks, 1924 (ROM 784); *Dysganus peiganus* Cope, 1876 (AMNH 3974); *Edmontonia longiceps* Sternberg, 1928 (NMC 8531); *Euoplocephalus tutus* (Lambe, 1902) (NMC 0210; originally described as *Stereocephalus tutus*; the generic name *Euoplocephalus* was proposed by Lambe 1910, with *E. tutus* as type species); *Hoplitosaurus marshi* (Lucas, 1901) (NMNH 4752; originally described as *Stegosaurus marshi*; the generic name *Hoplitosaurus* was proposed by Lucas 1902, with *H. marshi* as type species); *Hylaeosaurus armatus* Mantell, 1833 (BM (NH) R3775); *Nodosaurus textilis* Marsh, 1889 (YPM 1815); *Palaeoscincus asper* Lambe, 1902 (NMC 1349); *P. latus* Marsh, 1892 (YPM 4810); *P. rugosidens* Gilmore, 1930 (NMNH 11868; same as *Edmontonia rugosidens* of Russell, 1940); *Panoplosaurus mirus* Lambe, 1919 (NMC 2759); *Pinacosaurus grangeri* Gilmore, 1933a (AMNH 6523); *Polacanthus foxii* Hulke, 1881 (BM (NH) R175; the generic name *Polacanthus* was first used by Huxley 1867, but without a type species or specimen indication); *Priconodon crassus* Marsh 1888 (NMNH 2135); *Priodontognathus phillipsii* Seeley, 1869, 1875 (SMC B53408); *Regnosaurus northamptoni* Mantell, 1848 (BM (NH) R2422; this species may not be an ankylosaur); *Sauropelta edwardsi* Ostrom, 1970 (AMNH 3032); *Scolosaurus cutleri* Nopcsa, 1928 (BM (NH) R5161); *Silvisaurus condrayi* Eaton, 1960 (KU 10296); *Stegopelta landerensis* Williston, 1905 (FMNH UR88); *Struthiosaurus transilvanicus* Nopcsa, 1915 (BM (NH) R4966).

The following casts of type specimens were examined:

AMNH 2062, cast of type of *Heishansaurus pachycephalus* Bohlin, 1953; AMNH uncatalogued cast of type of *Palaeoscincus costatus* Leidy, 1856; AMNH 2071, cast of type of *Peishansaurus philemys* Bohlin, 1953; CM 973, cast of type of *Pleuropeltis suessi* Seeley, 1881; AMNH 2074, cast of type of *Sauropites scutiger* Bohlin, 1953; AMNH 2070, cast of type of *Stegosaurides excavatus* Bohlin, 1953; CM 972, cast of type of *Struthiosaurus austriacus* Bunzel, 1871.

I have also examined the following specimens:

Referable to (?) *Acanthopholis*: BM (NH) R3774, 35280, 35282, 44581, 49917, 47234, 47234a; GSM JB201, JB202, JB203, JB205, JB206, JB231, JB254, 114581, 114582, 114583, 114584, 114587; SMC B55354–B55358, B55368, B55369, B55370, B55400, B55412, B55436–B55448, B55492, B55514–B55526, B55730, B55731, B55744, B55749, B55750, B55751, B55760–B55765, B55938.

Referable to *Ankylosaurus*: AMNH 5214; NMC 8880.

Referable to *Euoplocephalus*: AMNH 5211, 5216, 5223, 5245, 5266, 5337, 5403, 5404, 5406m, 5409, 5440, 5470; BM (NH) R4947; NMC 349, 2252, 2253, 8876, 31070, 31071, 31072, 31073, 31074; NMNH 7943, 11892, 19747; ROM 788, 813, 832, 833, 1920, 7761, 7763, 7764, 7765, 7766, 7767, 7770.

Referable to *Hylaeosaurus*: BM (NH) R133, R202, R202a, R203, R604a, R643, R695, R1106, R1107, R1875, R1876, R1926, 2047, 2123, 2125, 2188, 2193, 2220, 2417, 2484, 2511, R2538, 2583, 2585, 2587, 2596, 2602a, 2615, 3782, R4951, 28681, 28936, 28949, 34533, 36487, 36489, 36490, 36491, 36492, 36493, 36494, 36515, 36516, 36517, 37713, 37714, 39533.

Referable to *Lametasaurus*(?): AMNH 1959.

Referable to *Panoplosaurus*: AMNH 3072, 3076, 5381, 5665; NMC 317, 8529, 8879, 9492, 9790, 9966; NMC field no. 12–1921; PU 21178; ROM 1215, 3088, 3129, 3302, 3368, 3516, 20892.

Referable to *Sauropelta*: all specimens listed by Ostrom (1970, p. 104) and by Bodily (1969; specimen incorrectly assigned to *Hoplitosaurus*).

APPENDIX B

Listed below are all formations that have yielded ankylosaur remains, with references to important descriptions. An asterisk (*) preceding a formation denotes additional, undescribed ankylosaur material that I have personally examined.

Nodosauridae are present in the following formations (listed alphabetically):

EUROPE: Ajka Beds	Nopcsa, 1915, 1929.
Cambridge Greensand	Seeley, 1869, 1871, 1879; Nopcsa, 1923.
Chalk Marl	Huxley, 1867.
Middle Gosau Formation	Bunzel, 1871; Seeley, 1881; Nopcsa, 1918.
*Wealden Beds	Mantell, 1833, 1841, 1844, 1849, 1850; Owen, 1858; Hulke, 1874, 1881; Nopcsa, 1929.
NORTH AMERICA: *Aguja Formation	All undescribed.
Arundel Formation	Marsh, 1888; Lull, 1911; Gilmore, 1921.
*Bearpaw Shale	All undescribed.
Cedar Mountain Formation	Bodily, 1969.
Cloverly Formation	Ostrom, 1970.
Edmonton Formation (Mbr. A)	Sternberg, 1928.
*Hell Creek Formation	All undescribed, doubtful occurrence.
*Judith River Formation	Leidy, 1856.
Lakota Formation	Lucas, 1901, 1902; Gilmore, 1914.
Mowry Shale or Thermopolis Shale (position uncertain)	Marsh, 1889; Williston, 1905; Moodie, 1910; Lull, 1921.
Niobrara Formation	Wieland, 1909, 1911; Mehl, 1936.
Ojo Alamo Formation	Gilmore, 1919.
*Oldman Formation	Lambe, 1902, 1919; Sternberg, 1921; Russell, 1940.
Terra Cotta Clay	Eaton, 1960.
Two Medicine Formation	Gilmore, 1930.

ASIA: not present.

Ankylosauridae are present in the following formations (listed alphabetically):

EUROPE: not present.

NORTH AMERICA: *Edmonton Formation (Mbr. A, B, E)	Sternberg, 1929.
Hell Creek Formation	Brown, 1908.
*Judith River Formation	All undescribed.
*Oldman Formation	Lambe, 1902; Gilmore, 1923; Parks, 1924; Nopcsa, 1928.
*Two Medicine Formation	Gilmore, 1930.
ASIA: Djadochta Formation	Gilmore, 1933a; Maleev, 1954; Maryńska, 1971.
Iren Dabasu Formation	Gilmore, 1933b.
*Lameta Beds	Matley, 1923; von Huene and Matley, 1933; Chakravarti, 1934.
Upper Nemget Beds	Maleev, 1956; Maryńska, 1969.
Unnamed strata in the Peoples' Republic of China	Young, 1935; Bohlin, 1953 (many, possibly all specimens described by Young and Bohlin were never catalogued and have deteriorated or disintegrated since they were described: Academia Sinica pers. comm. 1977).

Fragmentary ankylosaur remains that could belong to either family are present in the following formations:

SOUTH AMERICA: 'Estratos con Dinosaurios'	von Huene, 1929.
NORTH AMERICA: Selma Formation	Langston, 1960.
Kirtland Formation	Gilmore, 1916, 1935.